Asian Herpetological Research 2011, 2(3): 169-175
DOI: 10.3724/SP.J.1245.2011.00169

Morphology of *Kaloula rugifera* and *K. borealis* Tadpoles (Anura: Microhylidae: *Kaloula verrucosa* Group) in China

Bing ZHOU[1,2,3], Pipeng LI[1,3*], Yuyan LU[3], Jing LIAN[3], and Zhengyan ZHOU[3]

[1] *Institute of Applied Ecology*, *Chinese Academy of Sciences*, *Shenyang* 110016, *Liaoning*, *China*
[2] *Graduate University of Chinese Academy of Sciences*, *Beijing* 100039, *China*
[3] *Institute of Herpetology and Liaoning Key Lab of Evolution and Biodiversity*, *Shenyang Normal University*, *Shenyang* 110034, *Liaoning*, *China*

Abstract The external morphology and internal oral features of the tadpoles of *Kaloula rugifera* and *K. borealis* are described in this paper. Similarities between these two larvae include external morphology, oral disc, internal oral features (floor and roof), terminal mouth, lateral eyes, single midventral spiracle, absence of keratinized jaw sheaths and labial teeth, absence of lingual papillae and postnarial arena, while the body of *K. rugifera* is bigger than that of *K. borealis* at stages from 36 to 39 and the number of papillae in the buccal cavity is 12–19 and 9–16, respectively in the two species. All the similarities and differences of the two species illustrate that the tadpoles within the family Microhylidae could be attributed to assistance in clarifying a certain taxonomic treatment in Microhylidae.

Keywords tadpole, external morphology, oral disc, internal oral feature, taxonomy

1. Introduction

The family Microhylidae includes approximately 476 species in eleven subfamilies with a cosmopolitan distribution (Frost, 2011). Twelve reports describing the oral cavity of the tadpoles in the family have been reported so far, such as *Mcirohyla butleri* and *M. heymonsi* (Chiang and Li, 1958; Wassersug, 1980; Inger, 1985; Wassersug and Pyburn, 1987; Chou and Lin, 1997; EcheverrÍa and Lavilla, 2000). The most conspicuous characters which differentiate Microhylidae from other families are the absence of keratinized jaw sheaths and labial teeth, spiracle single and midventral in the type Ⅱ tadpoles (Orton, 1953; 1957). The genus *Kaloula* consists of 15 species, of which 4 occur in China (Fei *et al.*, 2009).

Kaloula rugifera and *K. borealis* are commonly distributed in China, and they are both assigned to the *K. verrucosa* group (Fei *et al.*, 2009). This paper is devoted to the description of lentic, suspension feeding tadpoles of *K. rugifera* and *K. borealis*, including their external morphology and internal oral features. External morphological characters and especially internal oral features are very important in systematics of anuran amphibians (Wassersug, 1980; Chou and Lin, 1997; Li *et al.*, 2011). Herein, we describe the external morphology and internal oral features of the two species, which would be useful in analyzing systematics and phylogeny of the genus *Kaloula* in Microhylidae, as well as in identifying and monitoring these two species in the field.

2. Material and Methods

The descriptions provided in this paper are based on the tadpoles deposited in the Liaoning Key Lab of Evolution and Biodiversity, Shenyang Normal University, Liaoning, China. The tadpoles at the developmental stages from 36 to 39 (Gosner, 1960) were fixed and preserved in 10% formalin. After external features were examined and measured, the internal oral features were dissected and examined. The transparent internal structures of oral cavity were stained with Giemsa to add contrast.

---

* Corresponding author: Prof. Pipeng LI, from Institute of Herpetology and Liaoning Key Laboratory of Evolution and Biodiversity, Shenyang Normal University, with his research focusing on biodiversity, evolution, conservation and sustainable development of amphibians and reptiles.
E–mail: lipipeng@yahoo.com

Received: 26 July 2011 Accepted: 14 September 2011

The morphological terminology and labial tooth row formula (LTRF) followed McDiarmid and Altig (1999); the descriptions of external and internal features followed Inger (1985); the terminology of oral disc followed Altig (1970); and the terminology of buccopharyngeal cavity features followed Wassersug (1976). The measurements followed Lian (2009) and were measured with a digital hand caliper, including TL: total length, BL: body length, TAL: tail length, SN: snout-nasal axis distance, SO: snout-ocular axis distance, SS: snout-spiracle distance, SV: snout-vent distance, BW: maximum body width, BH: maximum body height, TH: height of tail, DFH: dorsal fin height, VFH: ventral fin height, TMH: tail muscle height, TMW: tail muscle width, IND: internarial distance, IOD: interorbital distance, ED: eye diameter, HLL: length of hind limb, ODW: oral disc width, and LTRF: labial tooth row formula.

Specimens examined

Kaloula rugifera: SYNU 08091 (15 specimens were examined), Shenyang Normal University, Shenyang, Liaoning, China.

Kaloula borealis: SYNU 05037 (6 specimens were examined), Shenyang Normal University, Shenyang, Liaoning, China.

SYNU = Shenyang Normal University

3. Results

The external morphology of the tadpoles of *K. rugifera* and *K. borealis* are strikingly similar to that of other species in the family Microhylidae, which have a single midventral spiracle and non-keratinized mouthparts [Orton's (1953) Type II]. The detailed morphometric data for the tadpoles at stages 36–39 are presented in Table 1.

3.1 Examined specimens of *K. rugifera* tadpoles Fifteen tadpoles of *K. rugifera* were examined in this study. Eight tadpoles at stage 36, two at stage 37 and five at stage 38, collected from Chengdu, Sichuan, China.

3.2 Description of the external morphology The following description is based on the tadpoles of *K. rugifera* at stages 36, 37 and 38 (Figure 1). From dorsal view: body oval or elliptic, with front part slightly flattened; snout broadly rounded; largest width at the two-thirds of body, 0.74 (0.67–0.81) times of body length; eyes located laterally, visible from below; interorbital distance larger than eye-snout distance, nearly equal to body width and about 2.57 (2.26–3.12) times of oral disc width. In lateral view: body nearly triangular, body height 0.55 (0.50–0.61) times of body length, and 0.75 (0.61–0.84) of body width; snout nearly triangular, but vaulted on dorsum; at stages 36–38, without nostrils, snout-nasal axis distance less than three-fifths of snout-ocular axis distance; inernarial 0.16 (0.14–0.19) times of interorbital; and nasolacrimal duct visible. From ventral view: spiracle medial, close to vent, free portion with an arched membrane, the inner wall attached to body wall; vent tube medial; tail almost lanceolate, tail length 1.92 (1.75–2.17) times of body length, tail height two-fifths of tail length; dorsal fin convex, higher than ventral fin; maximum height of tail found in the middle of tail length; tail musculature taller than dorsal fin and ventral fin in proximal three-fifths of tail, originating from body-tail junction; heights of dorsal fin and ventral fin nearly equal; and lateral line pore and glands not visible under a stereomicroscope during these stages. In life, dorsum and tail dark brown, no pigment; venter not transparent, proximal margins much darker; and in preserved specimens, the dorsum and venter black-gray.

Table 1 Morphometric data of *K. rugifera* and *K. borealis* tadpoles at stages 36–39 (in mm)

Term	*K. rugifera* (n = 15)	*K. borealis* (n = 6)
TL	33.95 ± 2.07	25.48 ± 2.61*
BL	11.62 ± 0.60	10.22 ± 0.61*
TAL	22.33 ± 1.68	15.26 ± 2.14*
SN	2.16 ± 0.27	1.63 ± 0.09*
SO	3.66 ± 0.34	2.94 ± 0.20*
SS	11.97 ± 1.37	8.77 ± 0.54*
SV	12.91 ± 1.37	10.99 ± 0.77*
BW	8.62 ± 0.63	7.02 ± 0.19*
BH	6.41 ± 0.48	4.82 ± 0.24*
TH	7.76 ± 0.47	5.04 ± 0.87*
DFH	2.86 ± 0.25	1.76 ± 0.35*
VFH	2.52 ± 0.24	1.75 ± 0.30*
TMH	3.46 ± 0.22	2.22 ± 0.17*
TMW	2.50 ± 0.31	1.77 ± 0.17*
IND	1.21 ± 0.13	1.34 ± 0.08
IOD	7.69 ± 0.34	6.88 ± 0.20*
ED	1.44 ± 0.12	1.25 ± 0.07*
HLL	3.01 ± 0.85	2.84 ± 0.77
ODW	3.01 ± 0.30	2.33 ± 0.08*

* indicates the level of significance: $P < 0.01$. All the data were analyzed by independent-samples *t*-test. The data are presented as mean ± SD.

At the oral disc terminus (Figure 2), tadpoles lack a keratinized jaw sheath and labial teeth, width of oral disc 0.26 (0.20–0.30) times of body length and two-fifths of body width; with no marginal papilla and jaw sheath, upper labium flat, slightly arched; lower labium in reverse "Ω" shape.

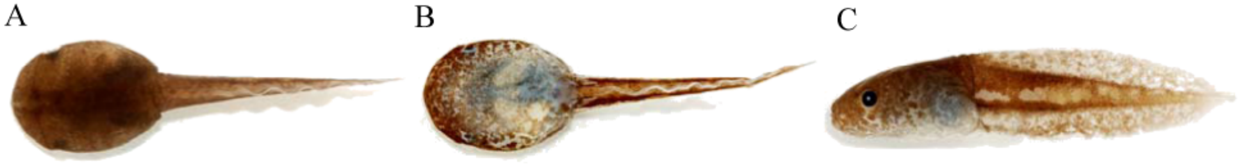

Figure 1 Tadpole of *K. rugifera* (at stage 36, BL = 11.42 mm and TL = 33.11 mm). A: Dorsal view; B: Ventral view; C: Lateral view. Scale bar = 5 mm.

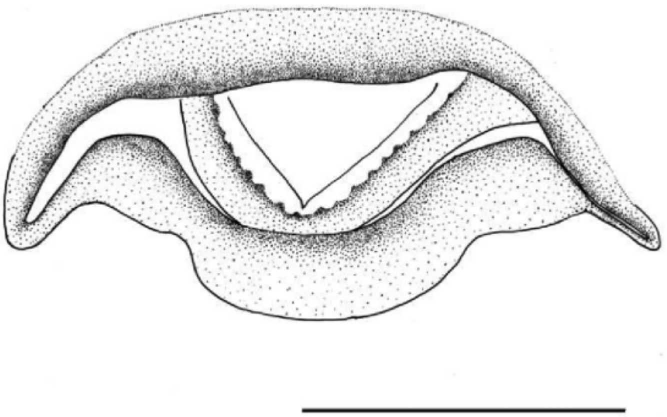

Figure 2 Oral disc of *K. rugifera* tadpole (at stage 36). Scale bar = 1 mm.

3.3 Description of the internal oral features Floor: infralabial flange "Ω" shaped, thin and smooth; prelingual arena very big, surrounding infralabial flange below, conical infralabial papillae marginally pustilate, located at each posterolateral corner; tongue anlage rounded, without lingual papilla; buccal floor arena with no clear boundary, with middle part slightly depressed; buccal pockets deep, elongate, oval, oblique, anterior margin with 1–2 conical papillae, directed to mid-posterior, at mid–distance between tongue anlage and glottis; posterior margin with 4–5 small papillae directed to pockets; glottis open, arising from center of buccal floor arena posterolateral; ventral velum discontinuous, wavy, separated by trachea medially, 2–3 small pustules found on margin, 3–4 long conical papillae arranged along the sides of the glottis, mid-forward directed to buccal floor arena; branchial baskets elongately oval, oblique, longer than wide, three gill chambers on each side; middle chamber much smaller, length of branchial baskets nearly equal to distance of tongue anlage and distance of posterior margin of ventral velum. Roof: prenarial arena broad, with a small, short, conical papilla, surrounded by 2–3 pustules; choanae rounded, internarial distance less than width of choanae; anterior narial wall not raised; a long, flat, nearly conical papilla covering choanae, with pustulose on the margin; 3–4 conical papillae found outside of choanae, oblique, the middle one much bigger; medial ridge nearly triangular or split peak, close to choanae, the height of medial ridge taller than bottom; lateral ridge flat, located laterally on medial ridge, with 1–2 tall conical papillae; postnarial arena absent; buccal roof arena nearly rectangular, with about 40–50 pustules; 2 tall papillae located posterolaterally, transverse; posterolateral ridge of arena with 7–10 pustules, oblique; glandular zone divided into two portions; and dorsal velum smooth, discontinuous (Figure 3).

3.4 Examined specimens of *K. borealis* tadpoles Six tadpoles of *K. borealis* were examined in this study. Three tadpoles at stage 36, two at stage 38 and one at stage 39, collected from Dandong, Liaoning, China.

3.5 Description of the external morphology The following description is based on the tadpoles of *K. borealis* at stages 36, 38 and 39 (Figure 4). From dorsal

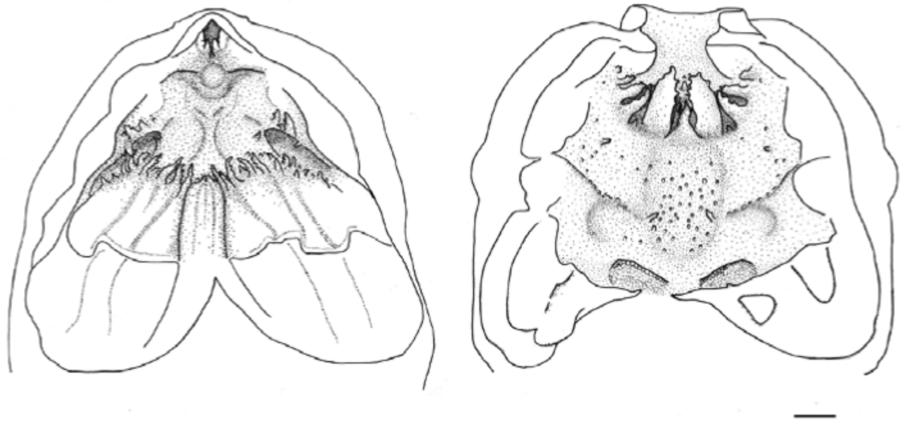

Figure 3 Floor (left) and roof (right) of buccal cavity of a *K. rugifera* tadpole (at stage 36). Scale bar = 1 mm.

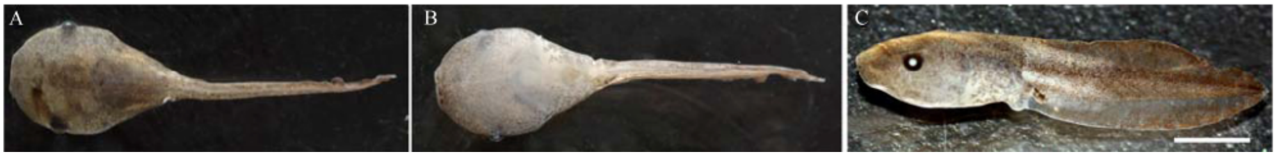

Figure 4 Tadpole of *K. borealis* (at stage 36, BL = 10.22 mm and TL = 25.48 mm). A: Dorsal view; B: Ventral view; C: Lateral view. Scale bar = 5 mm.

view: body circular or oval, snout broadly rounded on dorsum but trapezoidal in lateral profile; maximum width behind eyes; eyes located laterally at a place nearly one-third of body length, visible from below; eyeball diameter 0.12 (0.11–0.14) times of body length; interorbital distance larger than snout-ocular axis distance, almost equal to body width and about 2.95 (2.77–3.16) times of oral disc width. From lateral view: body triangular, largest at venter, body height 0.48 (0.44–0.50) times of length, and 0.69 (0.65–0.73) times of width; without nostrils at stages 36, 38 and 39; snout closely to eyes, snout-nasal axis distance three-fifths less than snout-ocular distance; inernarial 0.19 (0.18–0.21) times of interorbital; and nasolacrimal duct visible. From ventral view: spiracle medial, close to vent, inner wall attached to body wall, with outer arch membrane; vent tube medial; tail lanceolate, tail length 1.49 (1.24–1.67) times of body length, height one-third of tail length, maximum height found in the middle of tail length; upper fin arc, both margins tapering to acuminate tip; tail musculature taller than dorsal fin at proximal three-fifths of tail; origin of dorsal fin found at the end of body; and lateral line pore and glands not visible. In life, dorsal body and tail dark brown, without pigment; venter white or hoar, proximal margins much darker; and in preserved specimens, the dorsum and venter black-gray.

At the oral disc terminus (Figure 5), without keratinized jaw sheath and labial tooth, width of oral disc 0.23 (0.21–0.25) times of body length and one-third of body width; marginal papilla and jaw sheath absent, margin of upper labium nearly flat, slightly arc, and lower labium reversely "Ω" shaped.

3.5 Description of the internal oral features Floor: infralabial flange "Ω" shaped, flange thin and smooth; prelingual arena found inside of infralabial flange and below it, infralabial papillae small, flake, with 2–3 projections, located at each posterolateral corner of prelingual arena; tongue anlage set closely below prelingual arena, rounded, without lingual papillae; buccal floor arena without definite margin, depressed in middle; buccal pockets deep, oblique, middle of anterior margin with 1–2 small conical papillae, directed to mid-posterior, anterior margin distance equal to that between tongue anlage and glottis; posterior margin with 2–3 small papillae, directed to middle of pocket; glottis open; ventral velum not continuous, wavy, separated by trachea medially, 2–3 small pustules present in margin, 3–4 long conical papillae arranged along the sides of glottis; branchial baskets elongately oval, longer than width, three gill chambers on each side; the third chamber much larger, length of branchial baskets almost equal to distance of tongue anlage and distance of posterior margin of ventral

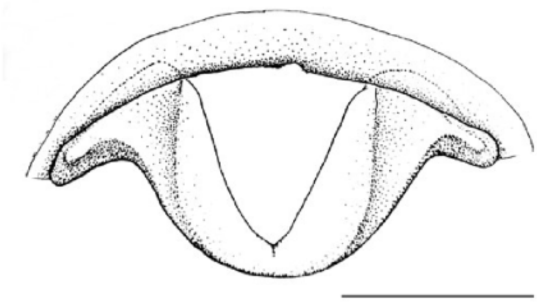

Figure 5 Oral disc of *K. borealis* tadpole (at stage 36). Scale bar = 1 mm.

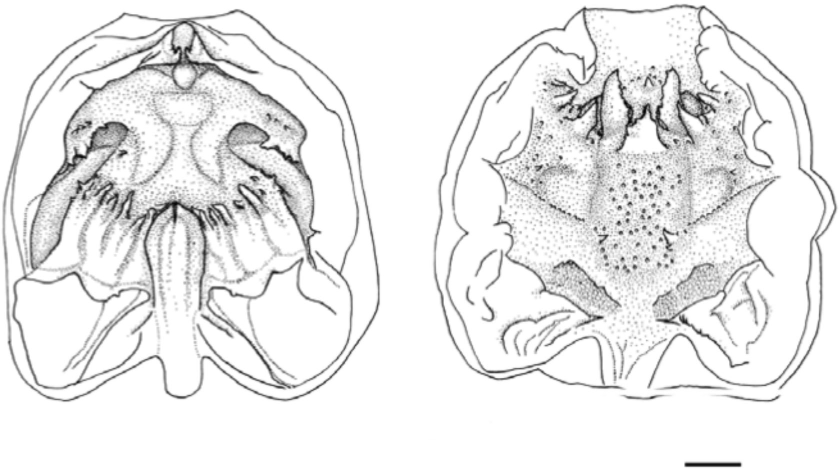

Figure 6 Floor (left) and roof (right) of buccal cavity of a *K. borealis* tadpole (at stage 36). Scale bar = 1 mm.

velum. Roof: prenarial arena broad, with a small, short and conical papilla in posterior portion, and 2–3 putules surrounded; choanae rounded, internarial diatance less than width of choanae; anterior narial wall not raised; pustules in middle; a pair of long, flat and nearly triangular papillae covering choanae, with pustulose on the margin; 2–3 conical papillae found outside of choanae, oblique, the middle one much bigger; medial ridge triangular, closely below choanae, the height of medial ridge taller than wide bottom; lateral ridge located laterally on medial ridge, flat and triangular with 1–2 small conical papillae on both sides; postnarial arena absent; buccal roof arena almost retangular, with about 45–50 pustules; 2 tall conical papillae located posterolaterally on buccal roof arena, transverse; posterolateral ridge of arena with 10–13 pustuloses, oblique; glandular zone divided into two portions; and dorsal velum smooth, discontinuous, without pustules (Figure 6).

4. Discussion

4.1 External morphology and oral disc There is very little information reported about the comparison of the tadpoles of *K. rugifera* and *K. borealis*. Gosner (1960) concluded that the tadpoles at stages 30–40 have relatively stable external morphological characters. Certain characters of the external morphology of the *K. rugifera* and *K. borealis* tadpoles show vary at stage 36 (Table 2). A single mid-ventral spiracle and non-keratinized mouthparts are the typical characteristics of microhylids [Orton's (1953) Type Ⅱ tadpoles]. The particular morphology of the two species of tadpoles suggests that microhylids are monophyletic and differ from all other anuran families (Chou and Lin, 1997). Of

Table 2 Comparison of external morphological characters between *K. rugifera* and *K. borealis* tadpoles in China

Characters	*K. rugifera*	*K. borealis*
Body shape	Elongately oval	Oval
Position of mouth	Terminal	Terminal
Position of eyes	Lateral	Lateral
Interorbital distance compared to snout-ocular distance	Big	Big
Position of spiracle	Close to vent	Close to vent
Position of vent	At end of body	At end of body
Tail shape	Lanceolate	Lanceolate
Shape of tail tip	Taper	Blunt
Origin of dorsal fin	Body-tail junction	At end of body
Gland	Absent	Absent
Life color	Dark brown	Dark brown
LTRF	Absent	Absent
Papillae in middle of upper labium	Absent	Absent
Papillae in middle of lower labium	Absent	Absent
Submarginal papillae	Absent	Absent
Jaw sheath	Absent	Absent

Table 3 Comparison of internal oral features of the *K. rugifera* and *K. borealis* tadpoles in China

Characters	*K. rugifera*	*K. borealis*
Floor		
Infralabial papillae shape	Flake	Flake
Lingual papillae	Absent	Absent
Buccal floor arena	Without margin	Without margin
Buccal floor arena marginal papillae	Absent	Absent
Pustules in buccal floor arena.	Absent	Absent
Buccal pocket	Oblique	Oblique
Buccal pocket anterior	1–2 conical papillae	1–2 small papillae
Buccal pocket posterior	4–5 small papillae	2–3 small papillae
Ventral velum	Interruption	Interruption
Gill chamber	Three every side	Three every side
Roof		
Prenarial arena shape	Wide	Wide
Prenarial wall	Unraised	Unraised
Postnarial margin	With 7–10 pustules	With 10–13 pustules
Postnarial arena	Absent	Absent
Medial ridge	Nearly triangular	Triangular
Buccal roof arena shape	Nearly rectangular	Rectangular
Buccal roof arena papillae	2 tall papillae	2 tall conical papillae
Pustules in buccal roof arena	40–50 pustules	45–50 pustules
Postero-lateral ridge	Obvious	Obvious
Glandular zone	Two portions	Two portions
Dorsal velum	Discontinuous	Discontinuous

the microhylid frogs in Taiwan and China, the tadpoles of *Microhyla butleri*, *M. steinegeri*, and *M. ornata* are typical microphagous tadpoles (Chou and Lin, 1997). Some researchers, such as Boulenger (1909), Dubois (1987), Parker (1934) and Duellman (1993) discussed the tadpoles of the genus *Microhyla* and the species *M. steijnegeri*. Our data on tadpole morphology prove that the characters of the species of *Kaloula* are strikingly similar to those of the species of *Microhyla*, which are single midventral spiracle and non-keratinized mouthparts [Orton's (1953) Type II].

4.2 Internal oral features The internal oral features of the tadpoles of *K. rugifera* and *K. borealis* are strikingly similar, differing only in buccal pocket anterior, buccal pocket posterior, postnarial margin, medial ridge, buccal roof arena shape, buccal roof arena papillae and pustules in buccal roof arena (Table 3). Liu (1940) proposed that the tadpoles with lumpy body, less well developed tail and weak mouth parts usually have the simpler type of taste organs, and found in still bodies of water while those living in running water generally possess a slim, streamlined body, well developed tail and strong mouth parts, as well as a complex set of taste organs. We found that the oral features of the both *K. rugifera* and *K. borealis* tadpoles are simple. The buccopharyngeal cavity of these tadpoles have few papillae, choanae blind depressions, and no lingual papillae, which play an important role in capturing food from stream water into the buccopharyngeal cavity, because these are suspension feeding tadpoles.

The main differences between *K. rugifera* and *K. borealis* tadpoles are that the number of papillae, which in *K. rugifera* are relatively more than those of *K. borealis*, and the pustules are opposite. Almost all the features appearing in *K. rugifera* and *K. borealis* tadpoles are also found in other tadpoles of Microhylidae, of which the internal oral features are known for *Microhyla bermorei* and *M. petrigena* (Inger, 1985), *Microhyletta stejnegeri* (Chou and Lin, 1997), and *Dematonatus muelleri* and *Elachistocleis bicolor* (EcheverrÍa and Lavilla, 2000).

The present knowledge on the internal oral features of the Microhylidae tadpoles is very limited, but the features of glottis' position, a terminal mouth and the lack of keratinized mouth assort microhylids into a unique family, which is consistent to Chou and Lin (1997). In addition, the reduction in size of infralabial papillae and the absence of lingual papillae (*M. butleri*, *M. heymonsi*, *M. ornata* and *M. steijngeri*; Chou and Lin, 1997; *Dermatonatus muelleri* and *Elachistocleis bicolor*; EcheverrÍa and Lavilla, 2000) may imply that these structures are not important in retaining some bigger particles in the buccal cavity. Starrett (1973) proposed that the microhylids are closely related to pipoid frogs (Orton Type Ⅰ), while Wassersug and Duellman (1984) thought that microhylids might have evolved from a ranoid-like frog based on a morphological link between microhylid and ranoid larvae (Orton Type Ⅳ). Therefore, our results could be attributed to that the external morphology and internal oral features of the two tadpoles would provide additional characters to assist in illustrating a certain taxonomic treatment in Microhylidae.

Acknowledgments We thank Jingyao LI for her assistance in experiment and species identification, and Qiang DAI from Chengdu Institute of Biology, Chinese Academy of Sciences for his help in collecting the tadpoles of *K. rugifera*. This study was financially supported by the National Natural Science Foundation of China (30470206, 30870276, 30970315) and the Setup-fund of the Specially Invited Professor of Shenyang Normal University to Pipeng LI.

References

Altig R. 1970. A key to the tadpoles of the continental United States and Canada. Herpetologica, 26: 180–207

Boulenger G. A. 1909. Description of four new frogs and a new snake discovered by Mr. H. Sauter in Formosa. Ann Mag Natl Hist, 8: 492–496

Chiang H. C., Li J. C. 1958. The study of the "taste organs" of the tailless amphibian tadpoles. Acta Sci Nat Univ Pekinensis, 2: 235–249

Chou W. H., Lin J. Y. 1997. Tadpoles of Taiwan. Natl Mus Nat Sci (Spec publ), 7: 1–98

Dubois A. 1987. Miscellanea taxonomica batrachologica (Ⅱ). Alytes, 6: 1–9

Duellman W. E. 1993. Amphibian species of the world: Additions and corrections. Mus Nat Hist, Univ Kansas (Specl publ), 21: 1–372

EcheverrÍa D. D., Lavilla E. O. 2000. Internal oral morphology of tadpoles of *Dermatonotus muelleri* and *Elachistocleis bicolor*. J Herpetol, 34: 517–523

Fei L., Hu S. Q., Ye C. Y., Huang Y. Z. 2009. Fauna Sinica. Amphibian. Vol. 2. Anura. Beijing: Science Press, 868–869

Frost D. R. 2011. Amphibian species of the world: An online reference.V5.5. Am Mus Nat Hist. Available from: http://research.amnh.org/herpetology/amphibian/index.php (Accessed on 31 August 2011)

Gosner K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica, 16: 183–190

Inger R. F. 1985. Tadpoles of the forested regions of Borneo. Fieldiana: Zool, 26: 1–89

Li P. P. , Liang J., Lu Y. Y. 2011. Tadpoles of Liaoning, China. Beijing: Science Press, 1-100

Lian J. 2009. Study on the Morphology of Anuran Tadpoles around Bohai Sea, China. Shenyang: Shenyang Normal University, 1–118

Liu C. C. 1940. Natural history study of west China amphibia. A. adaptations in tadpoles and adults. Peiking Nat Hist Bull, 15(2): 161–174

McDiarmid R. W., Altig R. 1999. Tadpoles: The Biology of Anuran Larvae. Chicago: Univ Chicago Press, 1–51

Orton G. L. 1953. The systematics of vertebrate larvae. Sys Zool, 2: 63–75

Orton G. L. 1957. The bearing of larval evolution on some problems in frog classification. Sys Zool, 6: 79–86

Parker H. W. 1934. A Monograph of the Frogs of the Family Microhylidae. London: Br Mus, 208 pp

Wassersug R. J. 1976. Oral morphology of anuran larvae: Terminology and general description. Occasional Papers of Mus Natl Hist, Univ of Kansas, 48: 1–23

Wassersug R. J. 1980. Internal oral features of larvae from eight anuran families functional, systematic, evolutionary and ecological considerations. Miscellaneous Publ, 68: 1–146

Wassersug R. J., Duellman W. E. 1984. The pseudohemisus tadpole: a morphological link between Microhylid (Orton type Ⅱ) and Ranoid (Orton type Ⅳ) larvae. Herpetologica, 40(2):138–149

Wassersug R. J., Pyburn W. F. 1987. The biology of the Peret' toad, *Otophryne robusta* (Microhylidae), with special consideration of its fossorial larva and systematic relationships. Zool J Linnean Soc, 91: 137–169

Starrett P. H. 1973. Evolutionary patterns in larval morphyology. In Vial J. L. (Ed.), Evolutionary Biology of the Anurans. Columbia, Missouri: Univ Missouri Press, 251–271